

Navigation system of the ant *Myrmica rubra* (Hymenoptera: Formicidae)

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Abstract

Foragers of *Myrmica rubra* were differentially conditioned to two olfactory and two visual cues. Their response to the visual cues was slight under light conditions at 110 lux. Conditioned workers negotiated mazes that were adequately provided with either olfactory or visual, or two kinds of cues. Under low light intensity, they performed better in presence of olfactory elements than in presence of visual cues and their performance was perfect when tested in presence of both two kinds of cues. They thus used similarly learned visual and olfactory cues; however, under low light intensity, they see poorly, thus rely less on visual cues than on olfactory cues. Indeed, in mazes provided with correct visual and incorrect olfactory cues, *M. rubra* workers were unable to find their way at 330 lux. At 110 lux, they incorrectly negotiated the mazes, since they could only slightly perceive the correct cues while perception of the incorrect cues was strong. In mazes provided with incorrect visual and correct olfactory cues, *M. rubra* workers again failed to find their way at 330 lux, since they perceived both correct and wrong cues simultaneously. At 110 lux, they correctly negotiated the mazes, since they slightly perceived the incorrect cues and strongly perceived the correct cues. In a final experiment, performed under very low light intensity and using mazes differently provided with cues, the previous results were confirmed. To summarize the navigation system of *M. rubra* foragers, it can be stated that these ants rely equally, as best as they can, on visual and olfactory cues. This conclusion is in agreement with the species' eye morphology, visual perception and usual biotope. The present work closes a series of studies on the visual and navigation system, as well as the biotope and eye morphology of *M. sabuleti*, *M. ruginodis* and *M. rubra* workers.

Key words: Conditioning, orientation, travelling, visual perception.

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Introduction

Foraging ants must be able to negotiate outside the nest and to return to it. It is well-known that they then use their area marking and trail pheromones, but they also rely on several kinds of visual cues, on path integration, odometry and odors to a lesser extent. Many species have now been investigated in detail, and a non-exhaustive list of the mechanisms the ants use for their foraging trips can be established. Firstly, ants may rely on their vision to navigate. *Pachycondyla apicalis* (see FRESNEAU 1985) and *Dinoponera gigantea* (see FOURCASSIÉ & al. 1999) clearly memorize one or several trajectories and their surroundings. *Formica* spp. memorize several bits of visual information inherent to their biotope (SALO & ROSENGREN 2001 and references therein). Wood ants of course primarily use vision while foraging (HARRIS & al. 2005, 2007). Ants can therefore use memorized landmarks they have previously encountered to navigate. *Cataglyphis cursor* has been used as a model by CHAMERON (1999) to establish the snapshot and sketchmap systems which explain the use of memorized visual cues (summarized in PASSERA & ARON 2005). Ants can also use, thanks to their visual perception abilities, cues from the canopy, celestial cues and / or polarized light. *Cataglyphis* spp. use celestial cues (WEHNER 1997) and polarized light (WATERMAN 1989, WEHNER 2003). *Pa-*

chycondyla tarsata (see HÖLLDOBLER 1980) and *Formica polyctena* (see SALO 1998) use cues from the canopy. Some desert ants can use the panoramic skyline to find their way (GRAHAM & CHENG 2009) as well as celestial cues (WEHNER 1997, 2009 and SCHWARZ & al. 2011 for *Melophorus bagoti*). *Gigantiops destructor* memorizes sequences of visual cues (MACQUART & BEUGNON 2007) and integrates them into pathways (SCHATZ & al. 1999) as well as the geometry and other features of the environment (BEUGNON & al. 2005, WYSTRACH & BEUGNON 2008). WYSTRACH & al. (2011) clearly showed that *M. bagoti*, an Australian desert ant, relies heavily on its vision to navigate and can learn landmark sequences. Working on this desert ant, NARENDRA (2007a, b) demonstrated that homing strategy may also essentially consist of path integration. This inevitably leads to a certain degree of imprecision, but ants compensate for this by locating the general area of the nest area, and searching intensely in this area. This behavior has been described by WOLF & WEHNER (2005) and later on by SCHULTHEISS & CHENG (2011). In the "Discussion" section, we again cite and elaborate on this point. Ants may also use olfactory cues for navigation although to a lesser extent than other cues (PASSERA & ARON 2005). For instance, *Cataglyphis fortis* complementarily uses odors for

orientation during travel (WOLF & WEHNER 2000). This species was recently shown to utilize odors as an additional cue for finding their nest even though they normally navigate using visual cues, a sun compass and odometry (STECK & al. 2009, 2011). As for odometry, indeed, such a system can be used, together with encountered visual and olfactory elements, to locate the nest or a food site. The ants then memorize the distance they have travelled (or the corresponding time or efforts). This has been demonstrated for *C. fortis* (see STECK & al. 2009 and references therein) as well as *Myrmica sabuleti* (see CAMMAERTS 2005a). Remembering locomotion reactions is also possible for ants on the move. This has been shown in *G. destructor* by MACQUART & al. (2006). The foragers then memorize their movements along a trajectory (turning left or right, going up, down or back and so on) and retrace their steps back along the trajectory.

Our studies provide further examples. We showed that foragers of *Myrmica sabuleti* MEINERT, 1861 primarily use odors to negotiate their trajectories (CAMMAERTS & RACHIDI 2009), although they are able to use visual cues in the absence of olfactory ones (CAMMAERTS & LAMBERT 2009). If the olfactory cues are incorrectly set in a maze, the ants initially respond to them but soon cease and switch to the available (correct) visual elements (CAMMAERTS & RACHIDI 2009). Later, we demonstrated that *Myrmica ruginodis* NYLANDER, 1846 foragers primarily use visual cues located above them (and not in front of them) to orient themselves, and that they neglect olfactory cues and continue to respond to visual cues even if they became obsolete. However, in the absence of visual cues or when they can no longer see, these ants rely on odorous elements to find their way and do so better under very low than under high light intensity (CAMMAERTS & al. 2012).

Myrmica sabuleti workers have rather small eyes, in comparison with *M. ruginodis* (see RACHIDI & al. 2008), poor vision (CAMMAERTS 2008) and nest in open land provided with small odorous plants, which is in agreement with their use of odors to travel. *M. ruginodis* workers have larger eyes (above reference) and a vision of better quality (these ants even distinguish different patterns of small luminous points, M.-C. Cammaerts, unpubl.); they nest around clearings under branches where some part of the sky is visible, which likewise is in agreement with their orientation system.

The common ant *Myrmica rubra* (LINNAEUS, 1758) lives on open grassland, has eyes of intermediate size compared to *M. sabuleti* and *M. ruginodis* (above reference), visual perception of middle quality (M.-C. Cammaerts, unpubl.). Its recruitment system has been known for quite some time (CAMMAERTS-TRICOT 1974). However, its navigation has yet to be investigated: the here related work seeks to fulfill this task.

The present study was conducted and is presented in the same manner as those on *Myrmica sabuleti* and *M. ruginodis* to ensure cross-comparison and readers' convenience.

Material and Methods

Collection, determination and maintenance of ants

The experiments were performed on six experimental colonies derived from large colonies collected in the Aise valley (Ardenne, Belgium) on an open grass land.

The species was identified using the key given by SEIFERT (1996) and DE BISEAU & COUVREUR (1994). *Myrmica rubra* workers have easily recognizable scape of antennae, with no lateral expansion as well as short spinae at the posterior part of the thorax (DE BISEAU & COUVREUR 1994: p. 27).

Each experimental colony was demographically identical and each contained a queen with about 500 workers and brood. They were maintained in the laboratory in artificial nests made of one to three glass tubes half-filled with water. A cotton-plug separated the ants from the water. The glass tubes were deposited in trays (52 cm × 37 cm × 87 cm; large enough to contain the three experimental apparatuses, see below), the sides of which were covered with talc. The trays served as foraging areas; food was placed in them, and the ants were trained, as well as tested on the floor of the trays (Fig. 1C).

Temperature was maintained at $20 \pm 2^\circ\text{C}$. Humidity was about 80% and remained constant over the course of the experimentation. The lighting had a constant intensity of 330 lux when caring for the ants (e.g., providing food, renewing nesting tubes) and during the training. During testing periods, the light intensity was adjusted to 330 lux, 110 lux or 15 lux (see below) using a dimmer.

Sugared water was permanently offered in a small glass tube plugged with cotton, and chopped cockroach was served twice a week on a glass-slide. Food was adequately provided during experiments since it served as a reward during training (Fig. 1C).

Experimental apparatus

To obtain and quantify olfactory differential operant conditioning, ants from each colony were trained with their own experimental apparatus. Afterward they were tested using another, similar apparatus (Fig. 1A). Again, each colony had its own test apparatus. The apparatus consisted of a piece of extra strong white paper (Steinbach®, 12 cm × 6 cm) orthogonally folded lengthwise to present a horizontal and a vertical part. A small glass tube (length: 7 cm; diameter: 1 cm) was inserted into a hole (diameter: 1.2 cm) cut in the middle of the vertical part very close to the base. The glass tube was placed in the foraging area with the opening in the middle of the apparatus. During training, the glass tube was filled with sugared water (the reward) and closed with a cotton plug, while a piece of onion and pieces of thyme were deposited on a glass slide cover slip (2.2 cm × 2.2 cm) located respectively on the left and on the right

Fig. 1: Experimental design and apparatus. (A) Differential olfactory conditioning: photo taken during test experiments with the two kinds of olfactory cues, onion (left) and thyme (right). (B) Differential visual conditioning: photo taken during experiments with the two kinds of visual cue, a blue (in front) and a yellow (behind) square affixed to a cube. (C, D, E, F, G) Study of the ants' use of cues to travel. (C) Entire experimental design: individual ants were differentially conditioned to olfactory and visual cues and tested (then not rewarded) in a maze with four points of choice provided with cues. (D) Maze with olfactory cues. (E) Maze with visual cues. (F) Maze with correct visual and incorrect olfactory cues. (G) Maze with correct visual and olfactory cues. →



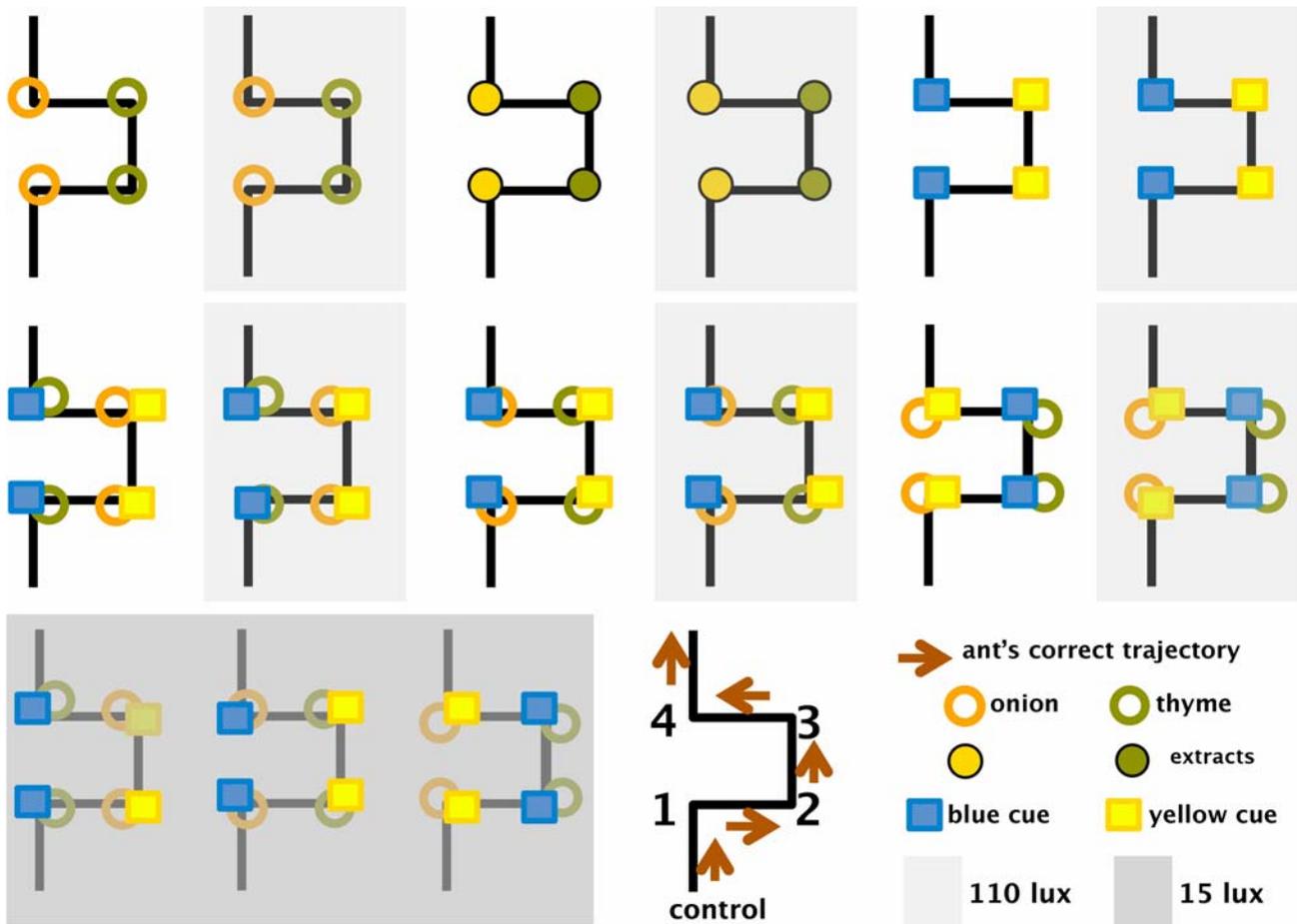


Fig. 2: Light intensities and cues used during the maze experiments. Full light equaled 330 lux; 110 lux and 15 lux were adjusted using a dimmer. A control experiment was performed before every second or third experiment. Ten ants from six colonies (total: 60 ants) were tested each time, and each ant had four choices to make (total: 240 potential choices).

horizontal ends of the experimental apparatus. In this way, the reward (sugared water, renewed when necessary) was located 4 cm to the right of the onion and 4 cm to the left of the thyme. Another glass slide cover slip was located in the middle of the apparatus in front of the opening of the sugared water glass tube (Fig. 1C).

The experimental apparatus used for testing was provided with onion or thyme or both cues depending on the experiments, and the glass tube was empty (i.e., no reward was given during tests), but closed with a cotton plug to prevent entry (Fig. 1A).

To obtain and quantify visual differential operant conditioning, ants from each colony were trained with their own training apparatus and then tested using another similar outfit so that, again, each colony had its own test apparatus (Fig. 1B). The apparatus consisted of a glass slide (2.6 cm × 7.6 cm) with a cube (2 cm × 2 cm × 2 cm) made of extra strong white paper (Steinbach®) placed at an end. On one face of the cube was a blue square (1.5 cm × 1.5 cm) and on the opposite face a yellow identical square. The cube was positioned on the glass slide so that the blue cue appeared to the left and the yellow cue to the right of the glass slide. The squared cues were cut from strong colored paper (Canson®) the colours of which had previously been analyzed for their wavelengths reflection (CAMMAERTS 2007, CAMMAERTS & CAMMAERTS 2009). During training, a piece of dead cockroach was tied to the end of the glass

slide where there was no cube, so at 4 cm from the cube (Fig. 1C). In this way, the reward was located 4 cm to the right of the blue visual cue, as well as 4 cm to the left of the yellow visual cue (Fig. 1C). During the tests, no meat was placed on the apparatus (Fig. 1B).

Remark. Sugared water was used as a reward during olfactory conditioning while meat was offered during visual conditioning. This arrangement was arbitrary; the inverse could have been done: using meat as a reward for olfactory conditioning and sugared water as a reward for visual conditioning.

To study the ants' use of olfactory and visual cues, workers were tested in mazes identical to those used to study the orientation system of *Myrmica sabuleti* (see CAMMAERTS & LAMBERT 2009, CAMMAERTS & RACHIDI 2009) and *M. ruginodis* (see CAMMAERTS & al. 2012). Each maze was made of white extra strong paper (Steinbach®), the floor width and the wall height were 2 cm and the distance between two turns (points of choice for the ants) was 4 cm. The maze had no ceiling and the walls were slightly covered with talc to prevent escape (Fig. 1C, D, E, F, G). A sheet of white paper of appropriate shape and dimension was placed on the bottom of the maze and renewed after each experiment. Depending on the experiment, either olfactory or visual or both kinds of cues were differently arranged inside the mazes as reported below and schematized in Fig. 2.

The light intensity, dimmed to 330 lux, 110 lux or 15 lux depending on the experiment performed, was measured using a Testoterm 0500 luxmeter (Testoterm GmbH & Co; D-7825, Lenzkirch).

Experimental protocol

To obtain and assess olfactory, as well as visual differential conditioning, ants were successively collectively trained (with two cues) during six days, then individually submitted to a first test. Thereafter, they were trained again for three days before being finally submitted to a second test.

Training. To train the ants, the appropriate experimental apparatus which was provided with cues and reward, was placed in the foraging area of the colony and relocated every five to 25 h. We avoided intervals of 12 h and 24 h between relocation to inhibit spatial and temporal learning (CAMMAERTS 2004a), as well as to prevent the establishment of chemical trails (CAMMAERTS-TRICOT 1974). When relocation took place, pieces of onion and thyme, as well as the reward were renewed when necessary.

Testing. To conduct a test or control experiment, the feeding apparatus used to train the ants was removed and replaced with an apparatus designed for the test procedure and which lacked any reward for the ants. Ant reactions were quantified as follows.

Olfactory conditioning. Two series of control and test experiments were performed to assess the ants' conditioning (Tab. 1). During each test experiment, the ants were counted 15 times for each of the six colonies, successively (a) in the presence of onion, on the left-half area of the apparatus; (b) in the presence of thyme, on the right-half area; (c) in the presence of onion and thyme, on the entire area (Fig. 1A). During each control, identical assessment took place but in the absence of any stimulus. For each experiment, the six mean values were calculated and the mean of the six mean values were established (Tab. 1). If the ants counted on the entire area is the sum of those counted on each of the two halves, then some ants were only conditioned to go to the right in the presence of onion and others to go to the left in the presence of thyme. Differential conditioning was successful when the ants counted on the whole area were less numerous than the sum of the two other counts.

The same manipulation was then conducted using aqueous extracts of onion and thyme (Tab. 1). Aqueous extracts of onion and thyme were obtained by placing pieces of these plants in glass tubes half filled with tap water and by warming the tubes to 100°C for 5 min in a double boiler.

Visual conditioning. Two series of control and test experiments were performed to assess the ants' conditioning (Tab. 2). During each test experiment, the ants present on the glass slide were counted 15 times, for each of the six colonies, successively using: (a) a blue cue attached to the cube placed on the glass slide; (b) a yellow cue attached to the cube on the glass slide; (c) a blue cue and a yellow cue attached to the cube on the glass slide (Fig. 1B). During each control, ants were similarly counted 15 times but only in the presence of cubes free of visual cue. For each experiment, the mean value of the 15 counts was calculated for each colony and the mean of the six mean values was established (Tab. 2). Differential visual conditioning was acquired when the number of ants responding to the cube provided with the two colored cues

was smaller than the sum of the numbers obtained for the cubes provided with only one visual cue (same reasoning as above). The same experiments were then conducted at 110 lux (Tab. 2).

To quantify the use of olfactory and visual cues by the ants, control and test experiments were conducted for all six colonies using mazes differently provided with olfactory and / or visual cues and under a given light intensity.

For an experiment, a maze provided with the respective cues was placed in the area of each used colony. Ten ants from each colony were, one by one, gently deposited inside near the entrance. After having moved through the maze, each tested ant was gently removed and isolated for the duration of the experiment in a polyacetate glass covered with talc to avoid testing the same individual twice during the same experiment (Fig. 1C).

The quantification of the ant's movement in the maze was identical to that used for studying the negotiation of mazes differently provided with cues by *Myrmica sabuleti* (see CAMMAERTS & LAMBERT 2009, CAMMAERTS & RACHIDI 2009) and *M. ruginodis* (see CAMMAERTS & al. 2012). Briefly, for each point of choice travelled by each of the 10 tested ants during one experiment per colony, we recorded if the ants made an incorrect (= 0) or a correct (= 1) choice. The ants' first response at each point of choice was taken into account, and not their possible second or later responses occurring when the ants retreated more than 4 cm. This quantification yielded for each colony the total number of correct choices out of 40 potential ones, and for the six colonies, the total number of correct choices out of 240 potential ones (Tab. 3). The score of the tested population was thus established for each experiment (Tab. 3). The numbers of ants having given zero, one, two, three or four correct choices were also assessed for each colony, then for the six colonies on which the same experiment was performed (Tab. 3); this assessment allowed statistical analysis.

Cues and lighting conditions used

Depending on the experiment, the light intensity was set to 330 lux, 110 lux or 15 lux and the cues placed in the mazes were either olfactory or visual or both kinds differently arranged. These lighting conditions and cues setting are schematically presented in Figure 2 and listed in Table 3.

Statistical analysis

For each of the two kinds of differential conditioning, the six mean numbers of reacting ants obtained for each test were compared to the corresponding six control mean numbers using the non-parametric test of Wilcoxon (SIEGEL & CASTELLAN 1989). Tables 1 and 2 give the values of N, T and P according to the nomenclature of SIEGEL & CASTELLAN (1989).

For each test experiment made using mazes, the distribution of the numbers of ants that gave zero, one, two, three or four correct choices was compared to the corresponding control distribution using the non-parametric χ^2 test (SIEGEL & CASTELLAN 1989). Note that the numbers of tested individuals were large enough for statistical purposes since ten ants from six colonies were used each time and each had four choices to make, doing so providing a total of 240 items. The choices observed for an experiment were considered not statistically different from the choices

Tab. 1: Differential olfactory conditioning to onion and thyme. Mean numbers of reacting ants (= those present on a given area) (for each colony: column two; for all of them: column three) during controls (in the absence of onion and thyme, on areas a, b or c) and during tests (performed at 330 lux, tests one and two with pieces of onion and thyme, test with extracts of these plants) in the presence of onion or extract of onion, thyme or extract of thyme, both stimuli or their extracts. In the fourth column, results of non-parametric tests of Wilcoxon between the six values obtained during a test experiment and the six corresponding control values (N, T, P according to SIEGEL & CASTELLAN 1989).

Experiment	Stimuli	Mean no. of reacting ants for colony						Mean Values	Statistics		
		1	2	3	4	5	6		N	T	P
control 1	a	1.53	2.40	2.13	0.73	0.20	0.33	1.22	–		
	b	1.87	1.07	2.40	0.40	0.87	1.60	1.37	–		
	c	3.13	3.47	4.47	1.00	1.00	1.27	2.39	–		
test 1	onion	4.27	5.80	3.13	2.73	1.33	1.80	3.18	6	21	0.016
	thyme	2.00	4.73	4.07	2.20	2.33	0.93	2.71	6	19	0.047
	onion + thyme	4.13	7.07	7.80	3.60	2.73	1.53	4.48	6	21	0.016
control 2	a	0.47	1.60	2.00	0.40	0.93	0.40	0.97	–		
	b	0.13	1.07	1.80	0.33	0.00	0.40	0.62	–		
	c	0.53	2.80	3.53	1.80	0.93	0.80	1.73	–		
test 2	onion	3.53	6.40	3.07	1.53	1.00	1.00	2.75	6	21	0.016
	thyme	1.67	6.33	5.33	1.40	0.73	1.00	2.74	6	21	0.016
	onion + thyme	4.47	8.27	7.33	1.73	1.20	1.47	4.08	6	20	0.031
control 3	a	0.47	1.47	2.67	0.33	0.27	0.53	0.96	–		
	b	0.60	1.20	1.33	0.20	0.33	0.27	0.66	–		
	c	1.00	2.67	3.66	0.53	0.60	0.60	1.51	–		
test with extracts	onion	3.13	4.33	3.40	1.73	1.33	2.33	2.19	6	21	0.016
	thyme	2.20	4.73	4.40	1.46	1.40	1.87	2.68	6	21	0.016
	onion + thyme	4.53	7.67	6.50	1.93	2.07	3.33	3.58	6	21	0.016

obtained during the control experiment (unsuccessful negotiation because total number of correct choices = total control number) when P was higher than the level of probability 0.05 divided by the number of tests based on the same control. This level of probability adjustment is the Bonferroni correction. The adjusted level of probability is given in Table 3 for each experiment. Values of P lower than the adjusted level of probability mean successful negotiation (total number of correct choices > total control number) or incorrect negotiation (total number of correct choices < total control number).

Results

Differential olfactory conditioning

After differentially conditioned to pieces of onion and thyme for six days and then for three more days, *Myrmica rubra* foragers statistically responded to one stimulus, to the other and to both stimuli (Tab. 1, test 1, test 2). The ants were actually differentially conditioned since their number in front of the two stimuli was lower (4.48; 4.08) than the sum of their numbers in front of one or the other stimuli (5.89; 5.49 respectively); thus, the same ants reacted to onion then to thyme in the course of the experiments.

The ants effectively responded to the odors of the stimuli since they statistically came toward extracts of one, the other, and both stimuli (Tab. 1, last line: control 3, tests with extracts). Once more, evidence of true differential conditioning is apparent in the fact that the ants' number in front of the two extracts (3.58) was lower than the sum of their numbers in front of one or the other stimuli (4.87).

Differential visual conditioning

After six days of training followed by three additional training days to a blue and a yellow square, *Myrmica rubra* workers statistically responded to one cue, the other and to both cues presented at the same time (Tab. 2, test 1, test 2). These responses occurred under the higher light intensity available in the laboratory (i.e., 330 lux). They were differentially conditioned since their number in front of a blue and a yellow square during each of the two tests (2.32; 3.49) was always lower than the sum of their numbers in front of one or the other of the two stimuli (2.89; 6.03 respectively).

When the same experiment was performed at 110 lux (after a supplementary training period), the ants only slightly and not statistically responded to one, the other and both stimuli (Tab. 2, last line: control 3, tests at 110 lux). The quality of their visual perception decreased under weak light intensity. On the basis of previous works (CAMMAERTS 2005b, 2007, CAMMAERTS & CAMMAERTS 2009), we may presume that, under rather low light intensity, *Myrmica* ants might be able to perceive the colors but not the shape of the presented visual cues.

Navigation in mazes

Use of olfactory cues (Tab. 3, line 1): After training to two different olfactory cues, *Myrmica rubra* foragers correctly negotiated mazes provided with both cues, those cues which were presented as pieces or as aqueous extracts. In both cases, the ants responded better at 110 lux than at 330 lux (78.33%, $\chi^2 = 36.50$, $df = 3$ vs. 70.83%, $\chi^2 = 18.98$,

Tab. 2: Differential visual conditioning to a blue and a yellow cue. Mean numbers of reacting ants (= those present on a given area) (for each colony: column two; for all of them: column three) during controls in front of a blank stimulus as well as during tests performed at 330 lux (tests one and two) or 110 lux (test three) in the presence of a blue, a yellow, a blue and a yellow cue. In the fourth column, results of non-parametric tests of Wilcoxon between the six numbers obtained during a test experiment and the six corresponding control numbers (N, T, P according to SIEGEL & CASTELLAN 1989).

Experiment Cue	Mean no. of reacting ants for colony						Values	Statistic		
	1	2	3	4	5	6		N	T	P
control 1 blank	0.07	0.73	0.47	0.47	0.60	0.00	0.39	–		
test 1 at 330 lux										
blue	2.00	3.00	1.07	1.00	0.53	2.00	1.60	6	20	0.031
yellow	0.60	3.00	1.80	0.67	0.67	1.00	1.29	6	21	0.016
blue + yellow	1.87	4.93	2.67	1.47	1.00	2.00	2.32	6	21	0.016
control 2 blank	0.33	3.27	1.73	0.33	0.00	0.53	1.03	–		
test 2 at 330 lux										
blue	2.33	10.20	3.20	2.00	0.87	2.20	3.47	6	21	0.016
yellow	2.00	6.67	4.13	1.00	0.47	1.07	2.56	6	21	0.016
blue + yellow	1.53	8.00	5.93	2.00	1.00	2.47	3.49	6	21	0.016
control 3 blank	0.47	2.73	1.40	1.00	0.00	0.33	0.99	–		
test 3 at 110 lux										
blue	1.33	4.47	1.73	0.47	0.47	1.33	1.63	6	18	0.078
yellow	2.07	4.27	1.80	0.33	0.60	1.00	1.68	6	18	0.078
blue + yellow	2.47	6.20	2.40	0.40	0.53	0.87	1.15	6	18	0.078

df = 3 for pieces of onion and thyme; 74.17%, $\chi^2 = 29.62$, df = 3 vs. 71.67%, $\chi^2 = 29.64$, df = 3 for aqueous extracts of onion and thyme).

It can be safely concluded that *Myrmica rubra* foragers use olfactory elements to find their way, especially when the light intensity is weak.

Use of visual cues (Tab. 3, line 2): After differential conditioning to a blue and a yellow square, *Myrmica rubra* workers correctly travelled through mazes provided with these cues. Their score was very high at 330 lux (82.50%, $\chi^2 = 41.60$, df = 3) but lower at 110 lux (63.75%, $\chi^2 = 9.78$, df = 3). This is in agreement with results of differential visual conditioning experiments (see above). When the light intensity decreases, *M. rubra* workers' visual perception lessens; at 110 lux, they can still see but not so well as at 330 lux (see the "Discussion" section) perceiving perhaps color but no longer the shape of the visual cues.

Relative importance of olfactory and visual cues, first part (Tab. 3, lines 3, 4, 5):

A (Tab. 3, line 3). *Myrmica rubra* workers were unable to negotiate a maze when it was provided with correct visual cues and incorrect olfactory ones. At 330 lux, visual perception was at its best and the ants thus relied on the correct visual cues. However, at the same time, they were able to perceive the incorrect olfactory elements. It was clear that they hesitated before attempting to move through the mazes and they failed to succeed negotiating it (61.25%, $\chi^2 = 5.48$, df = 3). At 110 lux, the ants saw with less acuity and relied more on the olfactory elements which were incorrectly set. The ants' score was therefore lower than the control one (37.50% vs. 51.25%); this difference was statistically significant ($\chi^2 = 11.66$, df = 3). These re-

sults underline the use of olfactory cues by *M. rubra* foragers for travel.

B (Tab. 3, line 4). *Myrmica rubra* workers moved perfectly through mazes correctly provided with visual and olfactory cues at 330 lux (86.25%, $\chi^2 = 55.24$, df = 3) as well as at 110 lux (85.42%, $\chi^2 = 53.63$, df = 3). Their scores were slightly higher than during experiments using either one or the other of the cues (Tab. 3, lines 1 and 2). They thus use both cues, olfactory and visual, whenever possible and relied more on one when the other became less available.

C (Tab. 3, line 5). At 330 lux, ants were unable to find their way in a maze when it was provided with correct olfactory cues and incorrect visual ones (50.00%, $\chi^2 = 3.62$, df = 3). At 110 lux, their score was at the limit of being significant (63.75%, $\chi^2 = 8.68$, df = 3). They perceived and used the correct olfactory elements but were largely influenced by the incorrect visual cues which they could still slightly perceive.

Occurrences of 330 lux and 110 lux in nature: Light intensity was assessed in the course of a cloudless summer evening. During the day, the light intensity was considerably higher than that available in the laboratory. During the evening, at a certain hour, the light intensity rapidly decreased; the light intensity was 700 lux, 130 lux, 75 lux and 15 lux at 21h 30', 22h, 22h 10' and 22h 30' respectively. Thus, the light intensity equaled 110 lux only from 22h 03' to 22h 04'. Later, it continued to decrease, but never equaled zero. Of course, the particular hours depend on the season. The same events (in an inverse order) occur at early morning (R. Cammaerts, pers. comm.). Ants' eyes might adapt in response to the rapid variation of light intensity occurring in nature (see the "Discussion" section).

Tab. 3: Foragers' navigation in mazes differently provided with learned cues (first column, Fig. 2). Responses of ten ants from six colonies were noted which allowed to define the numbers of ants that gave zero, one, two, three or four correct choices (column two), the total number of correct choices (column three) and so, the score of the tested population (fourth column). Last column: results of non-parametric χ^2 tests between the control and the experimental distributions. α = the adjusted level of probability according to the Bonferroni correction; P = the obtained level of probability; NS = not significant results at the adjusted level of probability. Red rectangles: These values are lower than the control ones.

Experiments	No. of ants that made					Correct choices among 240	Score %	Statistics
	0	1	2	3	4			
Olfactory cues								
control 1	5	11	23	19	2	122	50.83	–
onion + thyme 330 lux	0	4	14	30	12	170	70.83	$\alpha = 0.025$ P < 0.001
onion + thyme 110 lux	0	2	7	32	19	188	78.33	$\alpha = 0.025$ P < 0.001
control 2	1	16	26	14	3	122	50.83	–
extracts 330 lux	2	3	9	33	13	172	71.67	$\alpha = 0.025$ P < 0.001
extracts 110 lux	0	1	16	27	16	178	74.17	$\alpha = 0.025$ P < 0.001
Visual cues								
control 3	4	12	24	16	4	124	51.67	–
blue + yellow 330 lux	0	1	7	25	27	198	82.50	$\alpha = 0.025$ P < 0.001
blue + yellow 110 lux	1	9	17	22	11	153	63.75	$\alpha = 0.025$ P < 0.01
A Correct visual + wrong olfactory cues								
control 4	4	14	21	18	3	122	51.25	–
experiment 330 lux	0	7	26	20	7	147	61.25	$\alpha = 0.025$ NS
experiment 110 lux	9	20	25	4	2	90	37.50	$\alpha = 0.025$ P < 0.01
B Correct visual + correct olfactory cues								
control 5	2	19	16	22	1	121	50.42	–
experiment 330 lux	0	1	6	18	35	207	86.25	$\alpha = 0.025$ P < 0.001
experiment 110 lux	0	0	6	23	31	205	85.42	$\alpha = 0.025$ P < 0.001
C Wrong visual + correct olfactory cues								
control 6	7	12	23	13	5	117	48.75	–
experiment 330 lux	2	17	23	15	3	120	50.00	$\alpha = 0.025$ NS
experiment 110 lux	1	7	20	22	10	153	63.75	$\alpha = 0.025$ P \approx 0.025
Experiments at 15 lux								
control 7	6	15	21	13	5	116	48.33	–
experiment A	16	18	13	12	1	84	35.00	$\alpha = 0.017$ P \approx 0.05
experiment B	0	0	10	26	24	194	80.80	$\alpha = 0.017$ P < 0.001
experiment C	1	4	14	28	13	168	70.00	$\alpha = 0.017$ P < 0.001

Relative importance of olfactory and visual cues, second part (Tab. 3, line 6):

Experiments A, B, and C mentioned above were repeated at 15 lux.

A Ants incorrectly moved through mazes correctly provided with visual cues and incorrectly provided with olfactory elements. Their score equaled 35.00% which is, however, not highly statistically different from the control score of 48.33% ($\chi^2 = 7.50$, $df = 3$). Thus, they essentially used the incorrect olfactory information but continued to see visual cues (probably only their color) which were correctly set in the mazes.

B They could negotiate mazes adequately provided with visual and olfactory cues. Their score (80.80%, $\chi^2 = 41.68$, $df = 3$) revealed that they, of course, use the olfactory elements but relied also in part on visual cues since they could negotiate the mazes better than using olfactory elements alone (Tab. 3, line 1).

C When confronted at 15 lux with correct olfactory elements and incorrect visual cues, *M. rubra* workers could find their way (70.00%, $\chi^2 = 20.28$, $df = 3$). Once more, they essentially used the correct olfactory information (and could thus correctly move through the mazes) but continued to be influenced by the incorrect visual cues which

they could still slightly perceive (and thus moved not so well than in the presence of correct visual cues). That poor vision at low light intensity is debated in the "Discussion" section.

Discussion

The present work aimed to define the use of olfactory and visual cues for travel by the foragers of the ant *Myrmica rubra*.

Regarding the method, the blue and yellow squares, as well as the pieces of onion and thyme, are artificial cues never encountered by the species in the field. They are "model" elements easy to manipulate in laboratory, and they allow comparison with previous studies (CAMMAERTS & LAMBERT 2009, CAMMAERTS & RACHIDI 2009, CAMMAERTS & al. 2012). Nevertheless, the ants learned these artificial elements in the course of collective operant conditioning, as they should have done in nature while foraging around their nest.

Myrmica rubra foragers use chemical trails once these are operational. But, before having found a food source and still when efficient trails exist (though then, to a lesser extent), they also use their vision and their olfaction to find their way, as shown in the current study. This study also defines that *Myrmica rubra* foragers similarly use olfactory and visual encountered cues to travel. However, they rely more heavily on olfactory elements than on visual cues when light intensity decreased below 120 lux. With even lower light intensities (e.g., 20 lux, 15 lux), the workers primarily used olfaction to find their way but continue to rely on their vision to a slight extent.

Based on previous studies on the workers' visual system in *Myrmica sabuleti*, *M. ruginodis* and *M. rubra* (see CAMMAERTS 2005b, 2007, 2008, CAMMAERTS & CAMMAERTS 2009, CAMMAERTS in press; M.-C. Cammaerts, unpubl.), we advance the hypothesis that, at high light intensities (e.g., 10,000 lux, 500 lux), *M. rubra* workers can discriminate filled shapes (but not very well hollow ones), since their eyes function in the apposition mode. At intermediate light intensities (150 lux, 50 lux), probably at about 100 lux, their eyes adapt themselves and function in the superposition mode. Presumably, the workers can no longer distinguish shapes (squares, triangles) but continue to perceive the colors until the light intensities are very low (a few lux).

The lapse of time during which natural light intensity changes from high to low depends, of course, on the season but is generally very short (less than an hour) in the countries inhabited by *Myrmica rubra*. In any case, *M. rubra* foragers are always able negotiate their trajectories; they use encountered odors when their vision is limited (early morning, evening, early night) and probably rely primarily on vision when odors are weak and / or difficult to discriminate.

Myrmica rubra inhabits temperate climates and nests in open grasslands in highly variable biotopes containing stones and several plants, such as Poaceae, Epilobium, Plantain, dandelion, chickweed, buttercup, Rumex. The diverse biotopes have a similar character in that they are rather highly illuminated, contrary to the usual biotopes of *M. ruginodis* and *M. sabuleti*.

The navigation system of *Myrmica rubra* appears therefore to be adapted to the species' usual biotope, as are the navigation systems of *M. sabuleti* and *M. ruginodis*. Let us recall that *M. ruginodis* essentially uses visual cues to travel

(CAMMAERTS & al. 2012) while *M. sabuleti* relies primarily on odors to do so (CAMMAERTS & RACHIDI 2009). The navigation system of the three species is also in agreement with the eye morphology of the respective species (RACHIDI & al. 2008), their subtended angle of vision (CAMMAERTS 2004b, in press) and their visual perception capabilities (CAMMAERTS 2008; M.-C. Cammaerts, unpubl.). In other words, an ant species will adaptively acquire an appropriate navigation system on the basis of its innate visual perception, as well as of its other sensory abilities. We have demonstrated this in the three *Myrmica* species we studied. Similar agreement between foragers' visual performances and navigational strategy has also been "found" (but not explicitly linked) by NARENDRA & al. (2007b) and SCHWARZ & CHENG (2011) in *Melophorus bagoti*.

Let us go on comparing our results to those of other researchers regarding the adaptive use of navigational skills by ants as well as about interspecific differences concerning such uses. Here we showed that *Myrmica rubra* relies more on odors when light intensity decreases. Intuition tells us that ants should exploit the most appropriate cues for their current circumstances. For such topics, the most pertinent comparison could be with the intensively studied desert ants although, in this case, skills relate not always to visual and olfactory cues but also to other elements facilitating navigation. NARENDRA (2007a, 2007b), then NARENDRA & al. (2007a) and NARENDRA & al. (2007b) have studied the homing strategy of the Australian ant *Melophorus bagoti*. This ant uses path integration, including memory of travelled direction and distance, but also landmark and panorama guidance. It therefore relies on all the elements its physiological abilities allow it to detect, as was also shown by SCHWARZ & CHENG (2011) in their work on the same species. Though the authors did not explicitly state the fact, they clearly showed that *M. bagoti* weighs more or less on one or the other of its navigational method that is on landmark sequential memory and on odometry memory depending on the length of the outbound trip. Moreover, if this ant species does not locate its nest entrance with precision using this information, it engages in a systematic search to find it (SCHULTHEISS & CHENG 2011). This systematic search has also been studied by MERKLE & WHENER (2009 and references therein) in the desert ant *Cataglyphis fortis*. These authors subsequently showed that ants adapt their systematic search to the distance from the nest they had foraged (the home vector) (MERKLE & WHENER 2010). We have never examined (though often observed) searching behavior of this kind in the three species of *Myrmica* we used, but we can draw some comparisons. Desert ants complete a gap in a navigational method (path integration) by using another palliative one (systematic search). *Myrmica ruginodis* normally uses its vision to navigate but, in the absence of visual cues, it uses olfaction. Conversely, *Myrmica sabuleti* uses odors to travel but, in the absence of olfactory information, it falls back on visual cues. As for interspecific differences, SCHWARZ & CHENG (2010) have pointed out such ones by studying the navigation system of two desert ants, *Cataglyphis fortis* and *Melophorus bagoti* which inhabit different biotopes, using the same experimental set-up. The latter species, nesting in visually rich environment, learn visual cues more efficiently.

Finally, our studies underline the fact that a given species' system of navigation depends not only on the parti-

cular species, but also on the actual light intensity and the available odors (in addition to other factors, such as temperature). A species with large eyes and good vision living in well-lit environments essentially uses its vision to navigate but can also rely on odors when doing so is more appropriate. A good example is *Cataglyphis fortis*, a desert ant which essentially relies on vision, but also on odors, to locate its nest (STECK & al. 2009). Other examples can be found in the here above given references (e.g., SCHWARZ & CHENG 2011) as well as in the work of NARENDRA & al. (2011). In fact, ants tend to use their whole toolkit of navigation skills, this depending on their different sensory abilities, and rely more on one skill when other ones are less available. The present work clearly points out this fact in *Myrmica rubra*.

As a conclusion, our contribution has consisted in defining the navigation system of three species of *Myrmica*, in consideration of their biotope, recruitment strategy, eye morphology, subtended angle of vision and visual perception. A summary of these works had been planned. But, examining then the olfactory and the visual learning of the three studied *Myrmica* species, we found that these types of learning differ between the species and are each time in accordance with the species' navigation system. These observations should be included in the planned summary. We so aimed to present all our results, previous and yet unpublished ones, in a future short review.

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